Sci Nat (2017) 104: 78
DOI 10.1007/s00114-017-1499-8

SHORT COMMUNICATION

Beyond colour: consistent variation in near infrared and solar reflectivity in sunbirds (Nectariniidae)

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Received: 6 June 2017 / Revised: 15 August 2017 / Accepted: 20 August 2017 / Published online: 4 September 2017

Abstract The visible spectrum represents a fraction of the sun's radiation, a large portion of which is within the near infrared (NIR). However, wavelengths outside of the visible spectrum that are reflected by coloured tissues have rarely been considered, despite their potential significance to thermal effects. Here, we report the reflectivity from 300 to 2100 nm of differently coloured feathers. We measured reflectivity across the UV-Vis-NIR spectra of different (a) body parts, (b) colour-producing mechanisms and (c) sexes for 252 individuals of 68 sunbird (family: Nectariniidae) species. Breast plumage was the most reflective and cap plumage the least. Female plumage had greater reflectivity than males. Carotenoid-based colours had the greatest reflectivity, followed by non-iridescent and iridescent melanin-based colours. As ordered arrays of melanin-filled organelles (melanosomes) produce iridescent colours, this suggests that nanostructuring may affect reflectance across the spectrum. Our results indicate that differently coloured feathers consistently vary in their thermal, as well as obvious visual, properties.

Keywords Iridescence · Thermal · Infrared

Communicated by: Alexandre Roulin

Electronic supplementary material The online version of this article (https://doi.org/10.1007/s00114-017-1499-8) contains supplementary material, which is available to authorized users.

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Introduction

Animal integuments display a broad diversity of colour patterns typically used for camouflage (Baker and Parker 1979) or sexual signalling (Dale et al. 2015). While most studies focus on the colours themselves, colour production mechanisms can affect non-colour-based properties. For example, in birds, melanin strengthens feathers (Bonser 1995), while psittacofulvins (red and yellow pigments in parrot feathers) may prevent bacterial degradation (Burtt et al. 2010). Few studies, however, have examined the thermal properties of these various colour production mechanisms.

Solar radiation that reaches the Earth's surface spans the ultraviolet to near infrared wavelengths (290–2600 nm). However, visible colour is a poor predictor of the total solar radiation absorbed by integuments of living organisms, because the visible wavelengths are only a small fraction of the thermally relevant radiation (Gates 1980). For example, dark materials can have either greater or lower heat loads than light materials when exposed to solar radiation (Walsberg et al. 1978). Thus, how differently coloured tissues reflect the sun's radiation is unclear.

Birds produce various colours using pigments and structural colours. Pigments produce colours by selectively absorbing visible light (Hill and McGraw 2006). Melanins produce blacks, browns and greys, whereas carotenoids produce oranges, yellows and reds. By contrast, periodic nanostructured tissues produce iridescent or non-iridescent structural colours through coherent light scattering. Nanoscale arrangements of

melanin-containing organelles (melanosomes) in feather barbules produce iridescent colours ranging from ultraviolet to red in birds. Whether the thermal properties of these different colour production mechanisms vary is largely unknown (but see Bosi et al. 2008), even though different reflectance patterns of coloured tissues can directly affect body temperature (Clusella-Trullas et al. 2007).

We examined solar reflectivity (the amount of reflected solar energy) of differently coloured plumage patches across 68 sunbird species (family: Nectariniidae). Although all birds are endotherms, sunbirds are thermolabile, meaning that their body temperatures vary somewhat with ambient conditions (Prinzinger et al. 1989). Nectariniidae consists of 147 species, distributed across Africa and much of the southern part of Asia eastwards to the Australo–Papuan region. These small (5–45 g) passerines inhabit a variety of ecosystems, ranging from open habitats, such as savannah or scrublands, to primary forests, occupying altitudes from sea level up to more than 4900 m (Cheke et al. 2017). Moreover, their plumage is extremely colourful, including melanin, iridescent, white and carotenoid-based colours. Thus, any differences in the amount of solar energy reflected by plumage (solar reflectivity) might have significant physiological effects. Here, we compared solar reflectivity (300–2100 nm) and near infrared (NIR) reflectance of sunbird plumage with respect to colour production mechanism, body location and sex. We predicted that darker plumage would reflect less solar radiation and thus that darker plumage patches and sexes (males) would be less reflective.

Methods

We measured reflectance across 300–2100 nm for 252 individuals from 68 sunbird species (Table S1) using a dual spectrophotometer and light source setup (Avantes Inc., Broomfield, CO, USA): AvaSpec-2048 spectrometer (300–1100 nm) and AvaSpec-NIR256-2.0TEC (1000–2100 nm) and AvaLight-DH-S deuterium–halogen light source and AvaLight-HAL-S-MINI light source connected to a quadrifurcated fibre optic cable and held at 90° using a RPH-1 reflection probe holder. Around 55% of solar radiation reaching the Earth's surface is within the near infrared (700–2600 nm), but solar energy beyond 2100 nm accounts for only 5% and has little effect on solar reflectivity (Smith et al. 2016). We measured the reflectance of the breast, back, cap and shoulder plumage patches for male and female specimens of each species at the Royal Museum for Central Africa in Tervuren, Belgium. We collected three measurements per colour per body region per specimen and measured multiple specimens per species (Table S1) largely following the methods of Smith et al. (2016) (see supplement for details).

From our spectra, we calculated average reflectance across the avian-visible (300–700 nm) and near infrared (701–2100 nm) ranges and solar reflectivity (300–2100 nm) following Smith et al. (2016) (see supplement). We calculated solar reflectivity as a percentage of solar radiation reflected by plumage patches (Eq. 1), which is a function of reflectance (I) and solar irradiance (S) across wavelengths (λ).

$$Solar\ reflectivity = \frac{S(\lambda)I(\lambda)d(\lambda)}{I(\lambda)d(\lambda)} \quad (1)$$

For the solar irradiance, we used the ASTM G-173 standard irradiance spectrum using the 1976 US standard atmosphere derived from SMARTs v. 2.9.2 (Gueymard 1995, 2001). Using atmosphere parameters for sub-tropical, tropical and mid-latitudes produced the same results. To examine how different colour production mechanisms influence near infrared reflectance and solar reflectivity, we classified plumage colours into four broad categories based on their likely production mechanisms: (i) lack of or low pigmentation (white colours), (ii) carotenoid-only colouration (red and yellow colours), (iii) non-iridescent primarily melanin-based colours (black, brown and olive colours) and (iv) iridescent structural colouration [7]. We found no likely examples of non-iridescent structural colours.

Statistical analysis

We used the Bayesian Markov chain Monte Carlo generalised linear mixed models to compare solar reflectivity and average near infrared reflectance (NIR) of coloured plumage patches across and within species while simultaneously controlling for phylogeny and repeated measures. Each model had either solar reflectivity or average NIR as the response and sex of the specimen, location of plumage patch (back, breast, cap and shoulder) and plumage colour category (i–iv) as fixed effects. We used random intercepts for species and for specimen ID to account for repeated measures on the same species and different body regions of the same specimen. To control for non-independence between species in our analyses and phylogenetic uncertainty, we downloaded 100 Hackett backbone trees from birdtree.org (Jetz et al. 2012), fit our models to each tree and combined our model estimates to account for error among trees. To measure variation in NIR reflectance after accounting for avian-visible reflectance, we calculated the difference between measured NIR reflectance and fitted values from a model of NIR reflectance against avian-visible reflectance and reported range values (differences between maximum and minimum values). To examine the relationships between brightness of the different types of plumage colours and their solar reflectivity, we fit an additional solar reflectivity model with all effects mentioned above and included average avian-visible reflectance (300–700 nm) and its interaction with plumage colour category and as fixed effects. We excluded

unpigmented (or white) patches from this model due to a small number of measured patches. For further details, see supplement.

Results and discussion

Both solar reflectivity and average near infrared reflectance (NIR) varied in similar ways across differently coloured plumage patches (Fig. 1). White plumage reflected 1.6–2.2 times the solar energy and had 6.6–12.7 times greater NIR than pigmented patches (Fig. 1b, c; Table 1). Carotenoid-based red and yellow plumages (Fig. 1b, c; Table 1) reflected 1.3–1.4 times the solar energy and had 4.6–6.1 times greater NIR than melanin-based non-structural and iridescent colours (Fig. 1b, c; Table 1). Primarily melanin-based non-structural colours had similar solar reflectivity, but 1.5 times greater NIR than iridescent plumage (Fig. 1b, c; Table 1). After accounting for avian-visible reflectance, NIR reflectance was more variable for melanin (27%), carotenoid (21%) and iridescent colours (20%) than white colours (7%). Solar reflectivity of all pigment-containing plumage increased linearly with greater avian-visible brightness, but the relative increase in solar reflectivity was greater for carotenoid and melanin non-structural colours than iridescent colours (Fig. 1d; Table S3). Avian-visible and NIR reflectances were moderately correlated (phylogenetic independent correlation 0.59), and there was approximately 26% variation in NIR reflectance after accounting for visible reflectance. Furthermore, when accounting for differences in avian-visible brightness, non-structural pigmentary colours had higher solar reflectivity than iridescent colours (Fig. 1d; Table S3). On average, female plumage had 1.2 times the solar reflectivity of male plumage (Fig. 2a; Table 1), but both sexes had similar variability in NIR reflectance after accounting for avian-visible reflectance (22%). Across the examined body regions, the breast plumage had the highest solar reflectivity, followed by the back plumage and shoulder plumage, whereas the cap plumage had the lowest solar

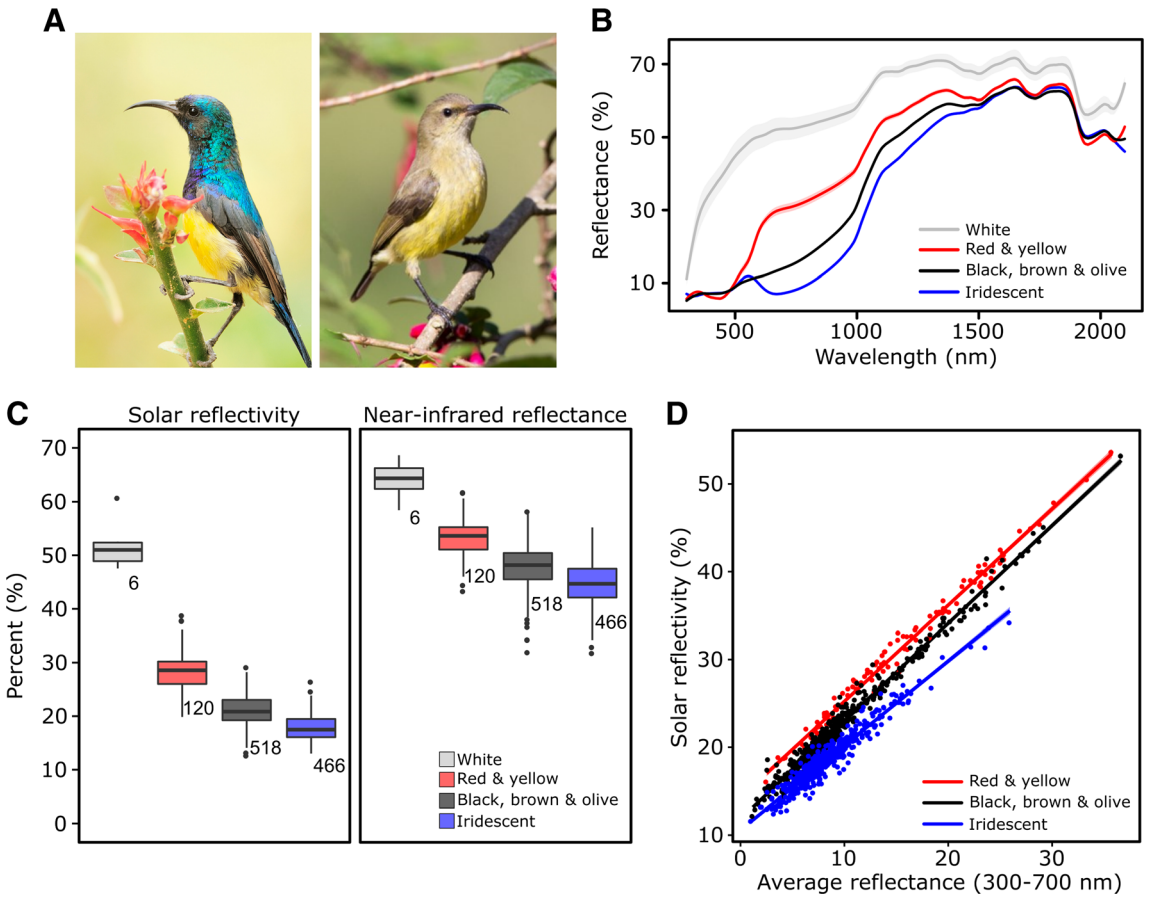

Fig. 1 Solar reflectivity and near infrared reflectance of sunbird plumage. **a** Male (left) and female (right) variable sunbirds, *Nectarinia venusta* (Shaw & Nodder, 1799). Credit: male, Wikipedia (CC BY-SA 3.0); female, Bob Hogeveen (Used with permission). **b** Spectrogram reflectance of different plumage colours. **c** MCMCglmm predicted percentages of solar reflectivity (300–2100 nm) and near infrared reflectance (700–2100 nm) of different plumage colours. Numbers are sample sizes of patches. **d** MCMCglmm predicted percentages of solar reflectivity as a function of average reflectance over bird-visible wavelengths

Table 1 Estimated differences and 95% credible intervals from the Markov chain Monte Carlo generalised linear mixed models comparing the solar reflectivity and near infrared reflectance of differently coloured plumage patches

Effect	Solar reflectivity Estimate [95% C.I.][a]	Near infrared reflectance Estimate [95% C.I.]
Sex		
Female–male	1.17 [1.12, 1.21]*	1.28 [0.30, 2.24]*
Body part		
Breast–back	1.07 [1.04, 1.11]*	− 0.72 [− 1.42, − 0.02]*
Breast–cap	1.27 [1.23, 1.31]*	5.36 [4.66, 6.08]*
Breast–shoulder	1.19 [1.15, 1.23]*	3.00 [2.31, 3.70]*
Back–cap	1.18 [1.15, 1.22]*	6.08 [5.40, 6.77]*
Back–shoulder	1.11 [1.07, 1.14]*	3.72 [3.05, 4.40]*
Shoulder–cap	1.07 [1.03, 1.10]*	2.36 [1.68, 3.05]*
Colour mechanism		
None–carotenoid	1.59 [1.35, 1.86]*	6.58 [3.04, 10.13]*
None–melanin	2.12 [1.81, 2.48]*	11.21 [7.67, 14.77]*
None–structural	2.19 [1.87, 2.56]*	12.73 [9.28, 16.28]*
Carotenoid–melanin	1.33 [1.27, 1.40]*	4.64 [3.58, 5.70]*
Carotenoid–structural	1.38 [1.32, 1.44]*	6.18 [5.21, 7.18]*
Structural–melanin	0.97 [0.93, 1.00]	− 1.55 [− 2.38, − 0.73]*
Phylogenetic variance	0.014 [0.005, 0.029]	16.28 [6.80, 31.62]
Residual variance	0.004 [0.002, 0.008]	4.78 [2.99, 7.66]

Significant effects are indicated by asterisks

[a] Estimates expressed as multiplicative differences, with exception of the variance components

reflectivity (Fig. 2b). After accounting for avian-visible reflectance, variability in NIR reflectance was similar across body parts (18–22%).

Reflectance of sunbirds in the UV-Vis-NIR region varied between body parts, sexes and colour production mechanisms. Specific feather colours may therefore have additional, potentially thermal, costs or benefits. While these data do not directly demonstrate these effects, they lay the groundwork for future physiological, behavioural and morphological tests that could have implications for the evolution of colourful plumage.

Between body parts, the caps reflected the least solar radiation and the breasts the most. This is interesting, since different parts dissipate heat at different rates depending on their surface area and feather density (Walsberg et al. 1978; Hohtola 2004). The breasts have the highest feather density and greatest insulation (Stettenheim 2000), but their high reflectivity may counterbalance these effects (and vice versa). By contrast, the dark cap is the most exposed and the least feather-dense area, and its high absorbance may mitigate this lack of insulation. In either case, this absorption could be

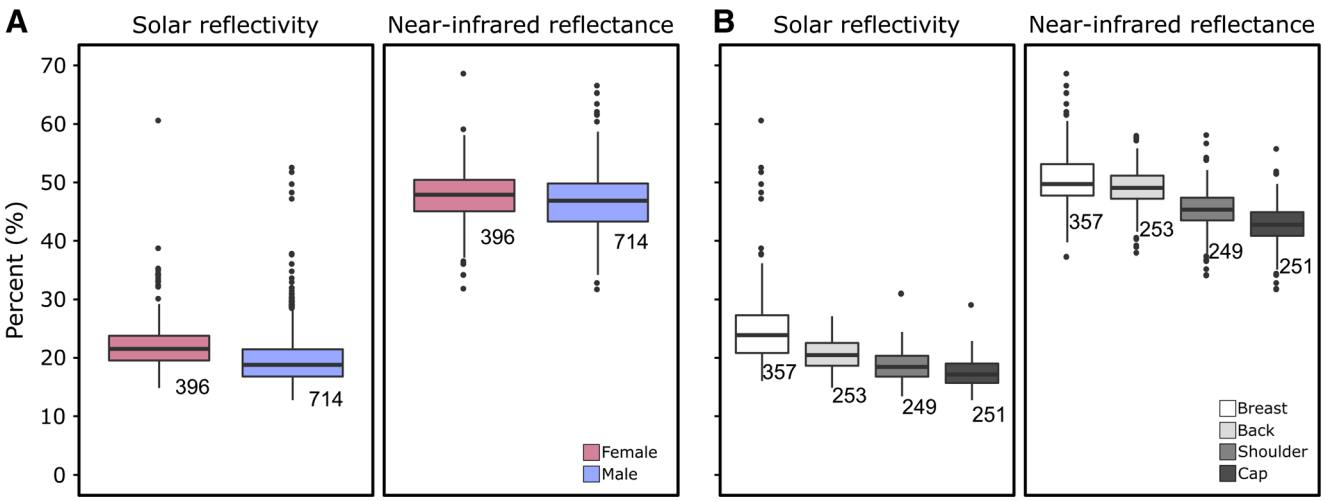

Fig. 2 Solar reflectivity and near infrared reflectance of plumage patches for **a** males and females and **b** different body patches. Numbers are sample sizes of patches

easily dissipated by convection, but the relationship between absorbance/reflectance and heat load is not straightforward (Walsberg et al. 1978) and requires considerable additional testing. Whether the colours of these parts that are frequently bright and displayed during courtship in birds have additional trade-offs or benefits could be explored using, for example, thermal imaging cameras and behavioural observations.

As predicted, light colours (particularly white) reflected more solar radiation than melanin-based colours, confirming previous results (Ward et al. 2007). More surprising, however, is that iridescent feathers reflected less radiation than melanin-based colours, as both use the same pigments (melanin), and iridescent feathers are brighter in the visible range than are melanin-based colours (Fig. 1b, d). The arrangement of melanosomes into ordered configurations (as opposed to their random orientation in melanin-based non-iridescent colours) may increase reflectance in the visible wavelengths by producing one or more reflectance peaks, but also lower reflectance in the NIR between 800 and 1500 nm. Melanosome organisation (or, potentially, their higher concentration (Maia et al. 2012)) within feather barbules might thus confer reflectance properties beyond colour. How NIR reflectance varies with angles of incidence and reflection will help elucidate whether iridescent feathers reduce heat intake through increased specular reflection and/or dynamically through body or feather positioning relative to the sun (Walsberg 1982). The nanostructuring of iridescent feathers may thus enable males to reduce heat gain costs of sexually selected feather colouration.

Finally, mirroring their human-perceived colour differences, the solar reflectivity of males and females dramatically differed. If we assume that sexual selection has largely driven male sunbird coloration while natural selection has driven female coloration, the highly reflective coloration of females may have been selected for thermoregulation in addition to camouflage. Since overheating is more energetically demanding than cooling (Hohtola 2004), selection may generally favour lower absorption by the feathers, particularly in the frequently tropical habitats of sunbirds.

Our aim was to examine the solar reflective properties of coloured feathers and infer their influence on thermoregulation. We have shown significant and consistent variation between sexes, body parts and colours which indicates that future research in this area is warranted. These studies should focus on how structural and pigment-based colour-producing mechanisms affect thermoregulation, particularly in thermolabile species like sunbirds. Furthermore, thermal imaging analysis and further investigations should concentrate on the reflectivity of different body parts to test the hypotheses generated in this work.

Acknowledgements We thank Michel Louette and Alain Reygal at the Royal Museum of Central Africa for access to specimens.
Funding information The work was funded by Fonds Wetenschappelijk Onderzoek grants G0G2217N and G07117N and Air Force Office of Scientific Research grant FA9550-16-1-0331 (MDS).

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